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THE SUBTERRANEAN INTERMEDIARY ORGANS OF *DIOSCOREA COTINIFOLIA* KUNTH: 2. ANATOMY OF THESE ORGANS IN COMPARISON WITH THAT OF A TYPICAL ROOT AND SHOOT

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Abstract

A comparison is made between the intermediary organs, (i.e. the tuber and cylindrical organs) and the roots and shoots. The most remarkable features of the root and the shoot are specially mentioned. Anatomically the intermediary organs have a rootlike feature but are in some respects similar to the shoot. This anatomical investigation, however, supplies enough evidence of the uniqueness of the specialised tuber system of *D. cotinifolia*, confirming the idea of it being intermediate between a typical root and a typical shoot. Detailed descriptions of the vascular elements are supplied.

Uittreksel

DIE ONDERGRONDSE INTERMEDIÊRE ORGANE VAN *DIOSCOREA COTINIFOLIA* KUNTH: 2. ANATOMIE VAN HIERDIE ORGANE IN VERGELYKING MET DIÉ VAN 'N TIPIESE WORTEL EN STINGEL

'n Vergelyking tussen die intermediêre organe (d.i. die knol en silindriese organe) en die wortels en stingels word getref. Die opvallendste kenmerke van die wortel en die stingel word spesiaal vermeld. Anatomies het die intermediêre organe 'n wortelagtige kenmerk maar kom in sommige opsigte ooreen met die stingel. Hierdie anatomiese ondersoek het egter genoeg getuienis van die uniekheid van die gespesialiseerde knolsisteem van *D. cotinifolia* gelewer om die idee dat dit intermediêr tussen 'n tipiese wortel en 'n tipiese stingel is, te onderskraag. Gedetailleerde beskrywings van die vaatelemente word voorsien.

I. Introduction

In 1977 Von Teichman und Logischen, Robbertse and Van der Schijff described the origin of the subterranean intermediary organs of *Dioscorea cotinifolia* Kunth. Simultaneously and independently Cartoni-Cretton (1977) made similar observations on the tuber of *Tamus communis* L., a close relative of the genus *Dioscorea*, and also found that the tuber originates from the hypocotyl.

The underground structures which were described for *D. cotinifolia* by Von Teichman *et al.*, (1977) were: (1) roots; (2) the *tuberous* intermediary organs; and (3) the usually long, *cylindrical* intermediary organs closely resembling roots. For the sake of brevity we will refer to them as roots, *tubers* and *cylindrical organs* respectively. The latter two which include the crown of the tuber, comprise the specialised tuber system which bears the adventitious roots. In this anatomical comparison of the intermediary organs with typical roots and the

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typical internodes of the aerial shoot (referred to as shoots) we provide further evidence of their unique nature.

Neither Archibald (1967) nor Ayensu (1972) described the anatomy of the underground organs of *D. cotinifolia* and since Ayensu mentioned that these organs were generally neglected, it is considered appropriate to describe their anatomy in detail here. Figures of the tracheary elements are not supplied because the figures published by Shah *et al.*, (1967) and Tan and Rao (1974) are considered to be adequate. For convenience a short introductory description of the root and the shoot is also provided.

II. Material and Methods

The material used, (see Von Teichman and Logischen *et al.*, 1977) was dissected and fixed in 6 % glutaraldehyde at 0 °C. The preparation was done according to Feder and O'Brien (1968). The monomer mixture however consisted of 96 % (v/v) hydroxyethyl methacrylate (that is, the 96 % HEMA was purified to remove most of the methacrylic acid); 5 % (v/v) polyethylene glycol 200 and 0,1 % (w/v) azobis-iso-butyronitrile. The 2 μm sections were cut with glass knives on a MT-1 Porter Blum ultramicrotome. Sections were stained with periodic acid—Schiff's stain (PAS) followed by toluidine blue (Feder and O'Brien, 1968). Staining for lipids was done with a saturated solution of sudan black B in 70 % ethanol, rinsing briefly with 70 % ethanol and mounting the wet sections in glycerine jelly.

Large tuber pieces and other similar material, were dehydrated in a tertiary butyl alcohol series. Paraplast (melting point = 56–57 °C, obtained in pellet form) was used for infiltration and embedding.

The dewaxed sections were also stained with toluidine blue. Small pieces of the organs were macerated by briefly heating in a mixture of 50 cm^3 concentrated nitric acid and 1 g potassium chlorate. After rinsing in water and subsequently in 50 % ethanol the material was stained with 1 % safranine 0 in 50 % ethanol. An ethanol rinse preceded mounting in glycerine.

The section used in Figure 2B was FAA-material cut free-hand, air-dried, mounted, sputter-coated with gold and photographed with a Philips SEM 500 at 12kV.

III. Observations and Discussion

1. *The root*

The uniseriate rhizodermis with root hairs, encloses an exodermis, a parenchymatous central cortex and an endodermis (Fig. 1A). The cortex cells outside the endodermis usually have thickened inner tangential walls (Fig. 1B). The pericycle is lignified especially adjacent to the phloem groups. The stele is polyarch with huge metaxylem elements lying scattered in the pith (Fig. 1A).

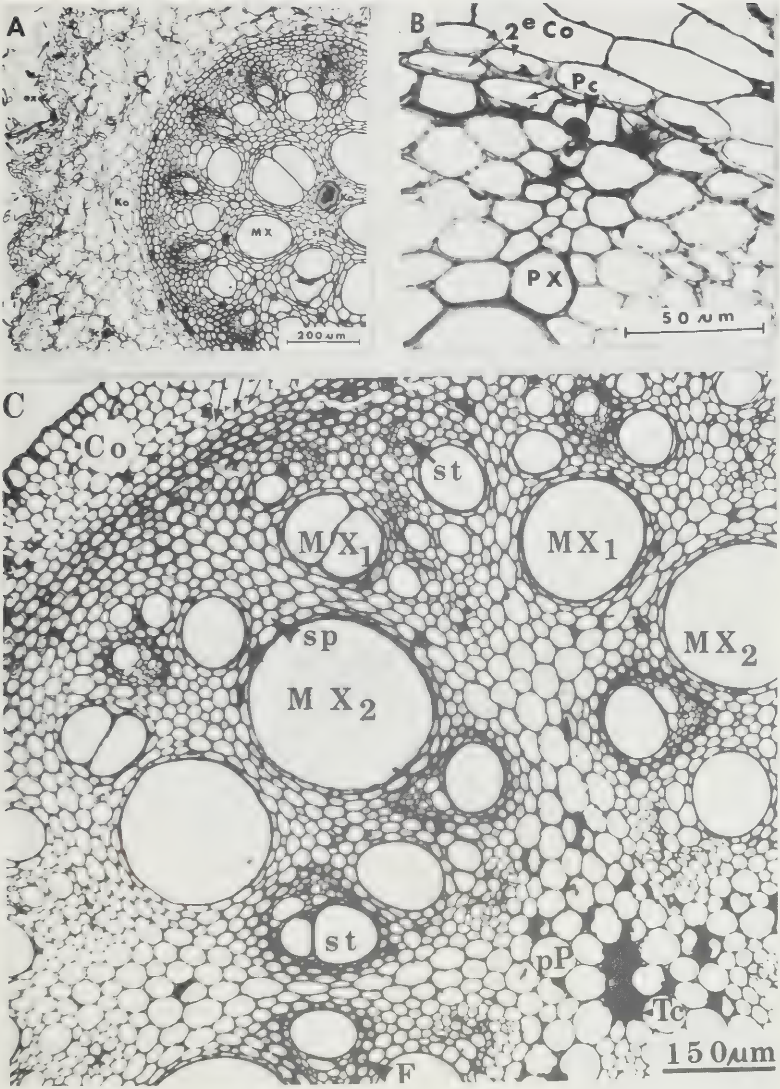

FIG. 1.

Transverse sections of the root and the shoot. A: Part of a mature root, exo—exodermis; Ko—idioblast; MX—metaxylem vessel; sP—sclerenchymatous parenchyma; B: A small part of a mature root, 2e Co—cortex layer outside endodermis; Pc—passage cells; PX—protoxylem vessel; C: Part of a mature shoot, small arrows—endodermoid layer; Co—cortex; F—fibre; MX_1 large metazylem vessel in common vascular bundle; MX_2 the same in the cauline vascular bundle; pP—parenchymatous pith; sp—sclerenchymatous parenchyma; st—sieve tube; Tc—tanniniferous cell.

2. *The shoot*

Inside the single-layered epidermis lies the cortex, the innermost layer representing the endodermoid layer. Inside this endodermoid layer is a mechanical tissue, of 6–8 layers of mainly lignified parenchyma, which encircles the vascular bundles. Several or single small common vascular bundles alternate with large cauline vascular bundles (Fig. 1C).

3. *A comparison of the intermediary organs with the root and shoot*

3.1 *The epidermis or outermost cell layer*

Unicellular structures resembling root hairs occur in the uniseriate epidermis of the young cylindrical organs (Fig. 2C).

Stomata and a cuticle are absent in this epidermis.

The epidermal cells of the root are dome-shaped with slightly thickened outer tangential walls. In mature cylindrical organs and tubers the epidermis has already been shed by the peripheral periderm.

The single-layered epidermis of the shoot consists of more or less spherical cells with rather thick, often lignified and pitted walls. Stomata are present and the thick (1,9 μm), often ridged cuticle stretches right into the substomatal chamber (Fig. 2A). The guard cells show distinct outer and inner ledges (Fig. 2A, inset). The subsidiary cells are usually distinctly radially elongated.

3.2 *The outer ground tissue and cortex*

Histochemical tests revealed no *suberin* or *lignin* in the hypodermal cells of young cylindrical organs. The outer ground tissue in these organs consists of thin-walled parenchyma. The phellogen, a continuous cambium, originates in about the seventh layer of ground tissue and initially forms two to three layers of phellem cells (Fig. 2C). Very little or no phelloderm is formed by the phellogen. In the tuber of *D. cotinifolia* the phellogen arises in the outermost ground tissue. This confirms the results of Martin and Ortiz (1963) on *D. floribunda* and *D. spiculiflora*. Other workers, like Bucherer (1889), state that the initials of the phellogen arise in the epidermis.

In the cylindrical organs of *D. cotinifolia*, the cell walls of the ground tissue between the epidermis and phellem become lignified. In other *Dioscorea* species this outer tissue is suberized (Sharma, 1974). The outermost tissue of old cylindrical organs and tubers of *D. cotinifolia* is a phellem of 6 to 12 layers.

In the cylindrical organs, a second lateral meristem is usually situated at about the tenth cell layer of parenchymatous ground tissue inside the phellogen (Figs 2C and 3). It is by no means a continuous cambium but merely a discontinuous meristematic zone. As a result of successive cell divisions within this zone, groups of small cells are formed which later differentiate into secondary vascular bundles (Figs 2C and 3). Secondary ground tissue is also formed by this meristem.

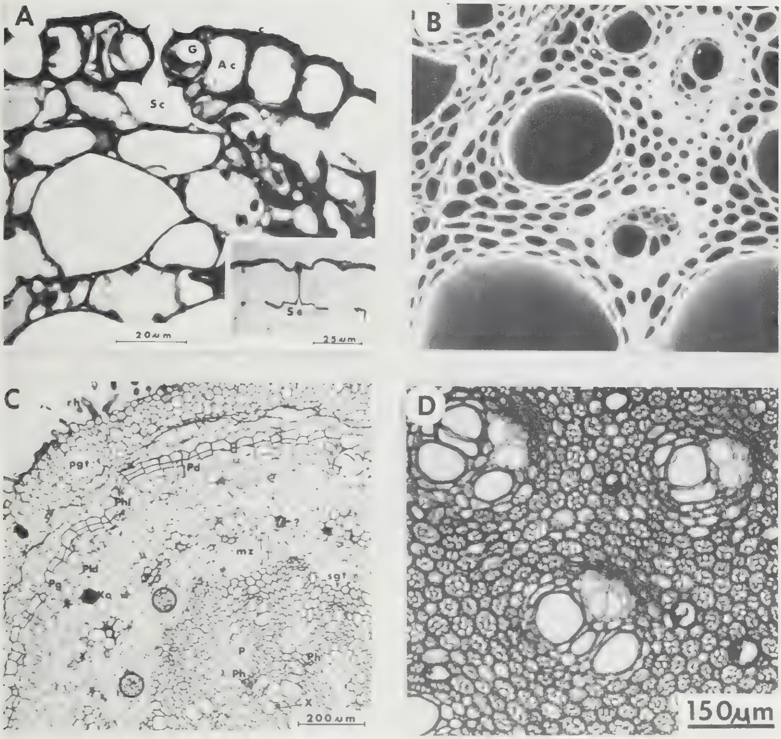

FIG. 2.

Transverse sections of the shoot and the cylindrical intermediary organ. A: Stomata of a shoot, Ac—subsidiary cell; G—guard cell; Sc—substomatal chamber, the inset is a GMA-section stained with Sudan Black B; B: Part of a cauline vascular bundle in the shoot showing the fibres surrounding the phloem unit (S.E.M. micrograph); C: A young cylindrical organ; Ko—idioblast with mucilage; mz—lateral meristem or meristematic zone; p—parenchymatous ground tissue; Pd—periderm; Pg—phellogen; Ph—phloem; Pld—phelloderm; rh—piliferous layer; sgt—sclerenchymatous ground tissue; X—xylem vessels or tracheids; circles—small groups of cells; D: Part of the sclerenchymatous inner ground tissue, filled with starch, and 3 vascular bundles in an older cylindrical organ.

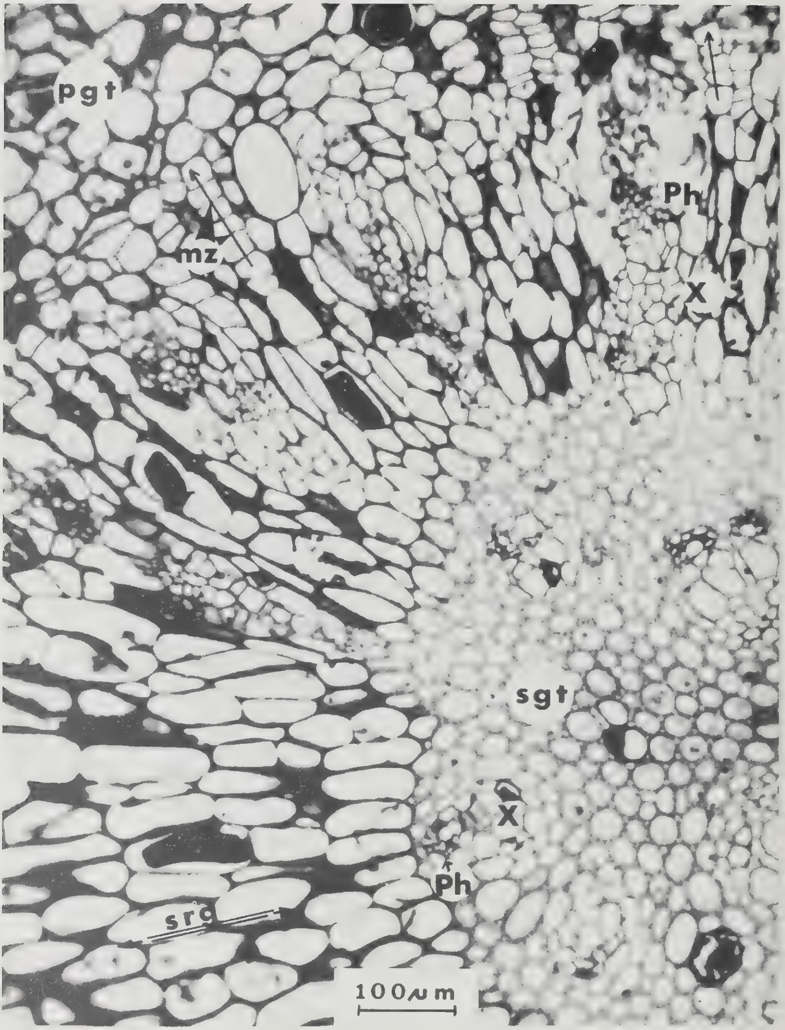

FIG. 3.
Transverse section of an older cylindrical organ, mz—lateral meristem; pgt—parenchymatous outer ground tissue; Ph—phloem unit; sgt—sclerenchymatous inner ground tissue; srg—cells radially elongated; x—xylem.

Tomlinson and Zimmermann (1967) described the origin of these secondary vascular bundles in the secondary ground tissue of monocotyledons as follows: "a vertical series of cambial derivatives divides longitudinally in various planes. From this prodesmogen strand tracheids, sieve-tubes and parenchyma differentiate". In the case of *D. cotinifolia* we have not confirmed their statement that the secondary vascular bundles usually do not include vessels.

Observations on very young tubers of *D. sylvatica* (Von Teichman und Logischen, 1973) confirmed the results of Bucherer (1889) and Martin and Ortiz (1963) regarding the origin of this lateral meristem. Martin and Ortiz stated, that the cambium as they called it, "is an extension and specialization of the primary thickening meristem". The latter begins very close to the promeristem in the tuber crown. This probably also applies to *D. cotinifolia* tubers. In the older tubers, however no distinct lateral meristem or meristematic zone can be distinguished.

Sharma (1974) also found that the "primary thickening meristem" is rather indistinct in mature tubers. In the apex of a young cylindrical organ of *D. cotinifolia* which had just started to tuberize, a distinct endogenous primordium (Fig. 4A) was noted within the meristematic zone. Such a primordium may develop into adventitious shoots, adventitious roots or secondary cylindrical organs (Von Teichman und Logischen *et al.*, 1977).

A section through the apex of this cylindrical intermediary organ shows that it is neither like a root nor like a shoot apex (Fig. 4A). No calyptra is present and the procambial strands are scattered. No leaf primordia are present and the lateral primordium (dark spot in Fig. 4A) is of endogenous origin. It is very close to the tip of the apex and its origin is slightly similar to that of root buds described by Peterson (1975). Our section is very similar to that of the tuber apex of *D. floribunda* (Sharma, 1980).

We therefore agree with Koch and Bruhn (1962) who stated that the tuber apex is not homologous with a root or a shoot apex, and that growth results from exceptionally actively dividing cells within the lateral meristem.

Martin and Ortiz (1963) observed that "the dorsal cortex of isolated tuber pieces is able to develop new shoot primordia, making possible the propagation of these species by tuber cuttings".

In some of the older tubers of *D. cotinifolia* a discontinuous band of sclereids is present in the inner part of the outer ground tissue. This ground tissue consists of thin-walled parenchyma with well-developed intercellular spaces. Tanniniferous cells and idioblasts, containing crystals in the form of raphide bundles surrounded by mucilage (henceforth referred to as idioblasts) occur throughout the ground tissue of all the intermediary organs.

The exodermal cells in the root are two to three times the size of the epidermal cells and a distinct continuous suberin lamella is present in their walls. Very large idioblasts occur in the otherwise thin-walled cortex while one or sometimes two cell-layers outside the endodermis usually have thickened inner tangential cell walls. In mature roots these cell walls become lignified (Fig. 1B).

In 1889, Bucherer already reported the presence of a characteristic layer or sheath ("Aussenscheide") in Dioscoreaceae roots just outside the endodermis, which he called "Schutzscheide". He also quite correctly mentioned that the degree of thickening of the cell walls of these cortex cells was related to the age of the root. The innermost cortical layers of *D. belizensis* are very similar to those of *D. cotinifolia* (Blunden *et al.*, 1963). The single layer of more or less rectangular endodermal cells have a suberin lamella in the walls except in the one to four passage cells opposite the protoxylem groups. In mature roots the U-shaped thickenings of the endodermal cells are lignified while the passage cells still have thin cell walls (Fig. 1B).

In the cortex of the subterranean part of adventitious *shoots* a periderm can be present (Fig. 4B). It is noteworthy that in these shoots, very simple, more or less collateral vascular bundles occur. The latter are very similar to those found in the seedling stem (compare Figs 5 and 6 in Von Teichman und Logischen *et al.*, 1977).

The cortex in the *stem* is usually about six to eight cell layers thick. The two to three layers of collenchymatous hypodermal cells are followed by chlorenchyma. Tanniniferous cells and huge idioblasts occur in the cortex. The innermost cortical layer is an endodermoid layer with lignified walls, the inner tangential walls being slightly thicker.

3.3 *The inner ground tissue and stele*

For the sake of convenience we regard the part of the ground tissue of the tuber and cylindrical organs in which the primary vascular bundles occur, as the inner ground tissue.

3.3 (a) *The inner ground tissue and vascular tissue of the tuber*

In the tuber the inner ground tissue is composed of parenchyma cells with thin cellulose walls and well-developed intercellular spaces. In all the tubers examined, starch occurs only in the storage parenchyma adjacent to the vascular bundles (Fig. 4D). Hand sections showed numerous simple starch grains of different sizes and forms packed into the storage parenchyma cells. The average measurements of the larger grains are 24 μm long and 15 μm in diameter. In the tuber of *D. belizensis* the starch grains are usually simple and up to 35 μm in diameter (Blunden *et al.*, 1963). Collateral vascular bundles lie scattered throughout the inner ground tissue (Fig. 4C). Anastomosis occurs freely between the vascular bundles. These anastomosing bundles usually have one large xylem group and two phloem groups lying more or less at their abaxial pole.

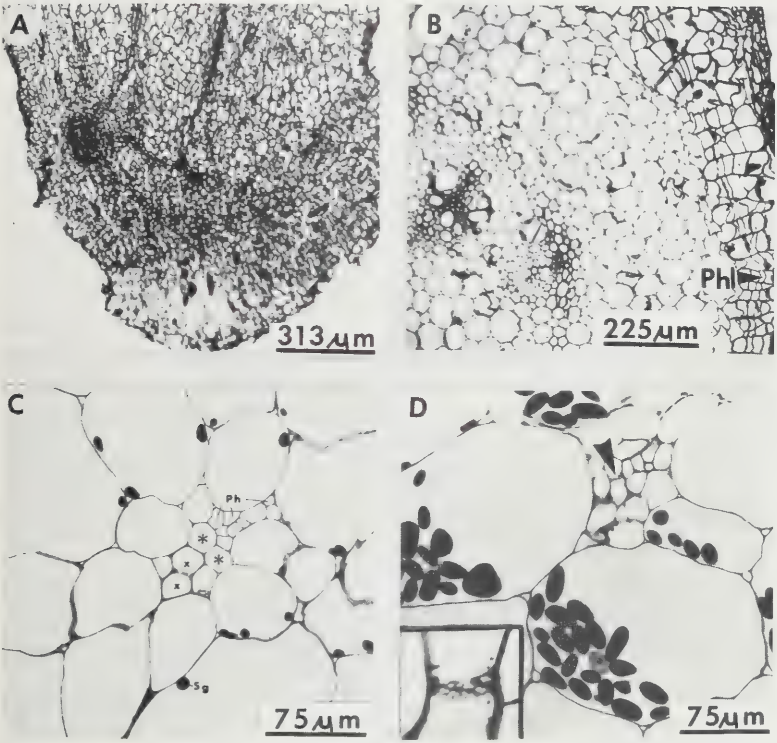

Fig. 4.

A: Longitudinal section of the tip of a very young intermediary organ showing scattered procambium strands and a young primordium; B: Transverse section of the subterranean adventitious shoot, showing the periderm, e.g. phellem (Phl), and simple vascular bundles; C & D: Transverse sections of tuber pieces, Ph—phloem unit, x—xylem; arrow in D—part of compound sieve plate, which is shown in the inset-magnification = 83 x, *—immature tracheids.

Detailed description of the vascular tissue of the tuber

During maceration the xylem elements in the cylindrical organs as well as in the roots and the shoot readily separated from the surrounding cells. When the same technique was, however, applied to the vascular bundles of the tubers, it was impossible to isolate the tracheids from the tightly adhering surrounding parenchyma and therefore no exact measurements could be made. It appears that vessel elements are absent and only tracheids are found in the tuber. The reason for the strong adherence of the surrounding cells to the tracheids is unknown.

In the tuber of *D. batatas, D. sinuata* and *Tamus communis* no vessels were found. However various types of tracheids occur, which also include tracheids with scalariform and reticulate thickenings (Bucherer, 1889). In *D. belizensis* the tracheids with bordered pits have a "wider diameter i.e. 21–*48*—*87*–111 μm" and are invariably longer than 500 μm (Blunden *et al.*, 1963). For *D. praehensilis* tubers Lawton and Lawton (1969) reported the presence of pitted vessels and other vessel elements varying in length and type of thickening. The tracheids are, however, more numerous than the vessels and have scalariform thickenings. According to Ayensu (1972), "of all the species investigated vessels were only found in *D. luzonensis*" tubers.

The average diameter of the large tracheids in *D. cotinifolia* tubers, as measured in transverse sections, is 24 μm, varying from 10 μm to 45 μm. The variation will henceforth be given in brackets. The estimated average length of some of the very long tracheids is 1 300 μm. Usually most of the tracheids are much shorter. According to the terminology of Esau (1965), the wall thickening in the tracheids is reticulate, scalariformly-pitted or pitted.

In the tuber (Fig. 4 D-inset) as well as in the cylindrical organs, the root and the shoot, compound sieve plates are present in the *large* metaphloem sieve tubes. Excepting the tuber, it was obvious that they occur on long oblique end walls. In *D. praehensilis* tubers, transverse, both simple and compound, i.e. oblique sieve plates occur in the narrow and wider sieve tubes respectively (Lawton and Lawton, 1969).

We agree with Koch and Bruhn (1962) that the general anatomy of the tuber (in their case *D. floribunda*) is very peculiar and differs markedly from that of the root and the shoot.

3.3 (b) *The inner ground tissue and vascular tissue of the cylindrical organ*

Even in young cylindrical organs, the inner ground tissue usually consists of storage parenchyma cells, the greater part having lignified cell walls (Fig. 2 C). Most of these cells, excepting the peripheral cells and those directly adjacent to the vascular bundle, are packed with starch grains (Fig. 2 D). The size of the starch grains varies considerably in cylindrical organs examined. This variability might be due to differences in age, time of collection and position in the plant. The average length of the starch grains is approximately 9 μm. In older cylindrical organs persisting for two or three growth seasons the whole inner ground tissue is lignified. The collateral vascular bundles which lie scattered in this tissue (Figs 2 C & D) are very similar to those in the tuber, and anastomosis also takes place frequently.

Detailed description of the vascular tissue of the cylindrical organ

Large metaxylem vessel elements: The average length is 1 714 µm (1 337 µm–2 475 µm) and the average diameter 54 µm (30 µm–75 µm). Perforation plates mostly oblique and usually scalariform or varying to scalariform-reticulate. Short sub-apical scalariform perforation plates also occur. Vessels with a perforation plate at the one end and a blunt and pitted end at the other end, also occur. The average length of perforation plates is 169 µm (112 µm–375 µm).

Tracheids: The average length is 1 618 µm (1 200 µm–2 100 µm) and the average diameter 33 µm (15 µm–70 µm). In comparison to the root, the cylindrical organs have relatively many tracheids. Their ends are often forked.

Fibres: The average length of the relatively few fibres that occur is 543 µm (375 µm–600 µm) and the average diameter is 13 µm (9 µm–18 µm).

Sieve tubes: The average diameter of the largest metaphloem sieve tubes as measured in transverse sections is 22,3 µm (9 µm–45 µm).

The pits in the large metaxylem vessels and tracheids of the cylindrical organs, the root and the shoot are bordered, and vary from scalariform, to mostly oval alternate or round alternate and sometimes opposite.

3.3 (c) *The stele of the root*

In the root a two to five layered pericycle is found. The cells bordering on the phloem have thickened lignified cell walls. The polyarch stele varies from 10-arch to 20-arch. The stele sometimes comprises up to two-thirds of the root diameter. The huge xylem vessels lie scattered in the pith, where idioblasts also occur (Fig. 1 A & B).

Detailed description of the vascular tissue of the root

Large metaxylem vessel elements: The average length is 3 795 µm (1 350 µm–7 200 µm) and the average diameter 83 µm (30 µm–120 µm). Perforation plates usually oblique and mostly scalariform to scalariform-reticulate. Their average length is 124 µm (30 µm–510 µm). Concave, relatively short perforation plates were also observed.

The widest vessels in *D. belizensis* have a diameter of "45–*105*—*144*–159 µm" (Blunden *et al.*, 1963). The average length and diameter of vessels in *D. sansibarensis* is "1 191 µm (range 820–5 000 µm) and 65 µm (range 24–180 µm) respectively. Pits on lateral walls alternate and opposite. Perforated scalariform plates mostly oblique, few horizontal. End plates 256 µm long (range 84–1 080 μm)" (Tan and Rao, 1974). The end plates in *D. sansibarensis* are also usually scalariform, or scalariform to reticulate (Tan and Rao, 1974).

Tracheids: The average length of the relatively few tracheids in the root of *D. cotinifolia* is 2 980 μm (2 260 μm–4 275 μm) and the average diameter 26 μm (15 μm–53 μm).

Fibres: The average length is 533 μm (337 μm–750 μm) and the average diameter 9 μm (7 μm–13,5 μm).

Sieve tubes: The average diameter is 49,6 μm (21 μm–75 μm). The sieve tube diameter in the case of *D. belizensis* is 15 to 36 μm (Blunden *et al.*, 1963).

3.3 (d) *The stele of the shoot*

In the internode a six to eight layered mechanical tissue of thick-walled lignified parenchyma ensheathes the central cylinder. The ground tissue between the vascular bundles is parenchymatous. Idioblasts and tanniniferous cells occur in the ground tissue and pith. One, or up to three common vascular bundles lie in alternation with the large cauline vascular bundles. The type of common vascular bundle which is usually present was described precisely by Ayensu (1972), namely "a V-shaped arrangement of metaxylem vessels and tracheids together with at least 2 phloem units terminating the flanges of the V, and a third phloem unit at the converging ends of the V," (Fig. 1 C). Apart from this "typical" type, atypical bundles were found in six of the internodes examined, where only *one* phloem unit occurs between the flanges of the V, while one large metaxylem vessel occurs at the base of the V (Fig. 1 C). Slight variations, other than this, were noticed in a few internodes.

The cauline vascular bundle which is present in all internodes examined, has *two* large phloem units on the inner side of the two large metaxylem vessels (Fig. 1 C). In this bundle a third phloem unit occurs at the abaxial side of the elliptical arrangement of metaxylem vessels and tracheids. The second most common type has four phloem units, three of these correspond to those described above and the fourth unit occurs just to the outside of and slightly between the two large metaxylem vessels (Fig. 2 B). In only two of the ten internodes examined a few cauline vascular bundles with two phloem units occur, namely *one* to the inside of the two large metaxylem vessels and one at the periphery. This bundle type was described by Ayensu (1972) for *D. cotinifolia*.

Detailed description of the vascular tissue of the shoot

Metaxylem vessel elements:

Although the internodal stem pieces used for maceration were up to 40 mm long, the ends of most vessel members were still cut off at one end. The longest metaxylem vessel element measured was 28 800 + μm. The shortest being 8 100 + μm, the approximate average length is 18 180 μm and the average diameter 131,6 μm (50 μm—240 μm).

In comparison Ayensu (1972) found the average diameter of the large vessels of *D. cotinifolia* to be 98 µm. Shah *et al.* (1967) described the internodal vessel elements of *D. alata*. These elements also vary greatly in size, the length of elements with foraminate perforations range from about 218 µm to 1 650 µm and the diameter from 13 to 16 µm; while elements with scalariform perforations vary from 1 000 to 7 700 µm in length and their diameter from 23 to 115 µm and those with reticulate perforations from 450 to 4 050 µm and 13 to 113 µm respectively.

Tan and Rao (1974) measured the diameter of the largest vessel in the internode of *D. sansibarensis* as 882 µm. In *Tamus communis, D. batatas* and *D. sinuata* scalariform perforation plates also occur on oblique end walls in the stem metaxylem elements. These elements also have linearly bordered pits in an alternate arrangement (Bucherer, 1889). The perforation plates of the large metaxylem elements of *D. cotinifolia* usually occur on long oblique end walls and are scalariform, mostly scalariform-reticulate and sometimes reticulate. Concave and even convex perforation plates also occur. The average length is 956 µm (210 µm to 3 000 µm). The number of cross bars in scalariform plates varies greatly and up to 144 cross bars per plate were observed.

Tracheids: Tracheids with annular, helical, reticulate and scalariform thickenings occur. Scalariformly-pitted, as well as pitted tracheids are also present. The approximate average length of the scalariformly-pitted tracheids is 1 298 µm (300 µm—2 400 µm). The average diameter of these is 16 µm (12 µm—23 µm). The shorter tracheids usually have bizarre shapes. Their length measures approximately 300 µm, and they usually have an alternate pitting. They were already described by Bucherer (1889) for the tuber of *Tamus communis*.

Fibres: The average length is 756 µm (390 µm—1 110 µm) and the average diameter 10 µm (7,5 µm—15 µm). Probably more fibres occur in the shoot than in the other organs. They appear to be concentrated around the phloem units (Fig. 2B). The pits in the end walls of some fibres are so closely spaced that they create the impression of a pitted plate.

Sieve tubes: In the cauline vascular bundles, on the inside of the two large metaxylem vessels, were measured in transverse sections. The average diameter of these sieve tubes in shoots with a relatively small diameter is 53 µm (30 µm—75 µm), while in shoots with a relatively large diameter it is 86,5 µm (60 µm—112,5 µm). In comparison Ayensu (1972) found the average diameter of the large sieve tubes of *D. cotinifolia* to be 28 µm.

Tan and Rao (1974) also found a definite correlation between stem diameter and vessel diameter in *D. sansibarensis*.

IV. CONCLUSIONS

Although the anatomy of the intermediary organs, i.e. the tubers and cylindrical organs, of *D. cotinifolia* Kunth seems to be unique, there is a characteristic which reminds one of roots, i.e. the piliferous layer. Characteristics which are similar to those of the seedling stem and subterranean part of adventitious shoots are: (1) the type of vascular bundle; and (2) the presence of a phellem.

The type of perforation plate in the large metaxylem vessel elements, the pitting of these elements and the tracheids of the cylindrical intermediary organs are similar to that of the root and shoot. These long scalariform perforation plates on the oblique end walls are considered to be primitive (Wagner, 1977). The intermediary organs, the root and the shoot have compound sieve plates on oblique end walls in the large metaphloem sieve tubes. The average diameter of the sieve tubes in the intermediary organs is about half that of the sieve tubes of the root and shoot. According to Cheadle (1948) sieve tubes with compound sieve plates are primitive. He also mentions that this type of sieve tube does not occur in the bulbs and corms of the monocotyledons.

That vessels are absent in the tubers and that the tracheids are ensheathed by strongly adhering parenchyma cells are unique features of these organs.

The intermediary organs are unique in the following respects: (1) the presence of a second lateral meristem or meristematic zone in the outer ground tissue; (2) in that the latter gives rise to secondary vascular tissue, ground tissue and endogenous primordia; (3) these primordia enable these organs to serve as vegetative reproductive organs, besides being storage organs; (4) the arrangement of the vascular tissue in scattered bundles, and (5) due to their origin from the hypocotyl, the tips of the very young intermediary organs resemble neither a root nor a shoot apex.

It remains to be mentioned, that the metaxylem vessel elements in *D. cotinifolia* shoots seem to be longer (28 800+ μm) than any previously described elements in *Dioscorea* spp.

The general anatomy of the intermediary organs is slightly similar to that of the *Dioscorea* rhizomes described by Ayensu (1972).

Some anatomical characters of the shoot of *D. cotinifolia*, i.e. (1) the rather bizarre shaped tracheids with alternate pitting and (2) the alternate pitting and scalariform perforation plates in the large vessels, are very similar to those of the stem of *Stemona tuberosa* Lour. (Govindarajalu and Rajasekaran, 1972).

All these interesting features are indications of a probable relationship between the Dioscoreaceae and the genus *Stemona* of the Stemonaceae (Roxburghiaceae) mentioned by Ayensu (1972).

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